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Autecology and the mycelium of a woodland litter decomposer

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Autecology has not been the forte of mycologists, apart from studies of certain commercially important species, notably pathogens. Central to an autecological approach is the need to know how the mycelium varies and is distributed under the influence of both genetic and environmental factors. Neglect of the mycelium has therefore gone hand in hand with the neglect of autecology. In this chapter, information on the mycelium of a single species, *Mycena galopus*, has been brought together to illustrate some of the themes developed elsewhere in the volume. Given the problems of identifying and isolating a mostly white and non-descript mycelium, a variety of approaches has been used by investigators, and the basidiocarp itself has often provided valuable, even if indirect, evidence.

M. galopus is one of many small agarics which grow on woodland leaf litter and produce troops of basidiocarps. It is a typical example of a saprotrophic fungus which colonises a spatially continuous resource with a diffuse spreading mycelium, in contrast to a wood decomposer such as *Tricholomopsis platyphylla* with far-ranging discrete cords (Thompson: Chapter 9). The morphology and habit of the basidiocarps are well known (Kühner, 1938; Smith, 1947; Charbonnel, 1977), but taxonomic monographs however excellent usually leave the vegetative mycelium to the imagination. The observations described here should begin to give an insight into the nature and ecology of the *whole* fungus.

Maas Geesteranus (1980) retained *M. galopus* (Tricholomatales) in the Lactipedes section of *Mycena* with other species possessing coloured or white latex in the stipe – a very useful diagnostic feature. Three varieties of this species all with white latex: *galopus*, *candida* and *leucogala* had been recognised by Pearson (1955). The last variety was

subsequently classified as a separate species (Dennis, Orton & Hora, 1960). In this chapter, '*M. galopus*' is assumed to be variety *galopus* unless stated otherwise, but *M. leucogala* is doubtfully a distinct species rather than part of one variable taxon. Forms intermediate between the typical black basidiocarps of *M. leucogala* on burnt ground and those of the grey brown or pure white varieties of *M. galopus* are common, and mycelia of the three taxa appear to be serologically identical (Chard, Gray & Frankland, 1983), but interbreeding has not been confirmed.

General characters and techniques

In culture, the mycelium is white or cream in colour, and appressed or shortly floccose with a silky or woolly texture (terminology according to Stalpers, 1978). Dark pigments are sometimes produced in unfavourable conditions, and mycelial threads of aggregated hyphae about 1 mm in diameter are formed on both nutrient agar and litter, but the mycelium and individual hyphae lack truly distinctive morphological features even when examined by scanning electron microscopy (Newell, 1980). It can be cultured satisfactorily on potato and malt extract media, but it is partially or wholly heterotrophic for thiamine (Lindeberg, 1946), and growth is much improved by additions of yeast extract and hydrolysed casein (Fries, 1949). Particularly good healthy production of mycelium has been obtained in Oelbe's (1982) synthetic medium, containing ammonium tartrate, malt and yeast extract (S. Morton & J. C. Frankland, unpublished); nitrates do not appear to be utilised when present as a sole source of nitrogen. From analysis of litter and mycelium stripped from it, phosphorus is probably the mineral element most likely to limit growth (Frankland, Lindley & Swift, 1978). These requirements could have far-reaching ecological implications for this fungus which may need to decompose considerable quantities of litter to obtain certain amino acids and other organic nutrients in limited supply.

Secondary mycelia have been produced in certain pairings of sib and non-sib monospore isolates, indicating a heterothallic system in which outbreeding was favoured, but some infertility between populations in different woodlands occurred. The 'bow-tie' phenomenon as described in *Stereum hirsutum* (Coates, Rayner & Todd, 1981) appeared frequently in sib matings, with uni- or bilateral dikaryons developing from the interaction zone (J. C. Frankland, unpublished).

Slight morphological differences between the homo- and dikaryons could be seen in culture, and the former were often more pigmented and slower growing. Although it is difficult to see any ecological significance,

there is also an intriguing account of on/off luminosity in primary and secondary mycelia of *M. galopus* by Bothe (1935); some homokaryons and synthesised dikaryons were luminous, and others not. However, Chard (1981) did not find any difference in the antigenicity of a homokaryon and dikaryotic isolates of this species in immunodiffusion tests.

Further information on the mycelium has come from experiments with axenic litter cultures, which bridge the gap between entirely artificial media and the field situation. It suggests that *M. galopus* in the absence of competitors is a relatively efficient fungus, capable of maintaining steady decomposition rates over long periods. Using hexosamine assay to determine mycelial biomass (impossible in the field), the efficiency (amount of mycelium produced per unit weight of substrate decomposed) on *Betula* and *Fraxinus* litter at field temperatures was 28–34% (Frankland *et al.*, 1978), compared with 37% on a glucose broth (Mikola, 1956). The long-term decomposition rate in similar model systems of *Quercus* litter at 11–15°C was calculated to be 0.1% day⁻¹ (Hering, 1982), and 0.3% day⁻¹ on *Fagus* at 25°C (Lindeberg, 1947).

More ingenuity is needed to differentiate the mycelium when competitors are introduced. Newell (1984a), after practice, achieved 95% accuracy in distinguishing young mycelia of *M. galopus* and *Marasmius androsaceus* on individual *Picea* needles in laboratory cultures by their growth form, including such features as closeness of the mycelial turf to the needle surface. In the field, she traced basidiocarps to their origin so that active mycelium could be located in the litter.

An antiserum which appeared in immunodiffusion tests to be species-specific has been raised against *M. galopus* mycelium (Chard, 1981). This could be useful in small mixed populations if it can be combined with fluorescent-antibody staining without cross-reactions. Membrane filtration was found to be a feasible means of estimating the presence and biomass of fluorescent hyphae of *M. galopus* when tests were made on *Quercus* leaves bearing basidiocarps (Frankland, Bailey, Gray & Holland, 1981).

Simple techniques which I have used for field identification include: plating of litter fragments on nutrient media (washing not always necessary) and comparison of the isolates with known cultures; tagging of mycelium grown on media containing a fluorescent brightener, Calcofluor White, for later retrieval; and incubation of litter to induce fruiting. The latter was a particularly successful means of identifying the mycelium on *Quercus* leaves. Abortive but recognisable basidiocarps containing white latex were produced after at least 8–12 weeks in a

damp atmosphere. In this way, the presence of the basidiomycete in a developing fungal community was based on recordings of the mycelium, not of the basidiocarps.

Habitats and resources

In distribution, *M. galopus* is predominantly a north temperate species, usually found in woodlands but also occurring in open habitats such as hedgerows and lawns. It was one of the species recorded most frequently on British Mycological Society forays in the UK over a 12-year period (Rayner, 1979). In North America, it is particularly abundant in the moist areas of the Pacific coast from Washington to California but rare in the mid-west and eastern states. More southern locations include Algeria, Madagascar (single record) and Mexico (R. Watling, personal communication), and a new variety, *mellea*, has been described in Australia (Grgurinovic & Holland, 1982).

The basidiocarps appear to be particularly vulnerable to exposure. Hering (1975) found that they were scarce in two of the highest natural *Quercus* woodlands (305–460 m) in the British Isles (with a relatively low tree line) compared with numbers in similar plant communities at much lower altitudes. I have also observed a marked difference in the frequency of fruiting in high- and low-level plantations of *Picea sitchensis*. It is not known to what extent the vegetative mycelium follows suit; it may well have a greater altitudinal range. Under Sitka spruce at 340 m (National Grid reference: SD 79/729972) the mycelium was always abundant, but fruiting was ubiquitous only in the occasional climatically 'good' year. In other years the basidiocarps could be found only in the lee of a tree stump or similar shelter from the prevailing wind. These observations could be explained by the presence of perennial mycelium more tolerant of, or more protected from, harsh environmental conditions. Hintikka (1964) suggested that *M. galopus* was one of the psychrotolerant species producing mycelium abundantly in Finnish forests in late autumn, and active in winter even under snow although capable of growth at 20–25 °C. This has been supported by the results of some *in vitro* experiments (Frankland, 1982; Newell, 1984a). Although the optimum temperature for growth of this species on solid agar media was 21–22 °C, it decomposed *Quercus* litter to a significant extent at 4 °C, grew at temperatures as low as –2 °C, and survived at –12 °C.

M. galopus is, as Parker-Rhodes (1954) described it, a 'quisquili-colous' woodland species. It is not associated with any particular soil

type, occurring as it does in a wide variety of broad-leaved and coniferous forests. In a study of *Pteridium* decomposition, it was found to be prominent on six different but adjacent soil types, including moder-type humus, mull and peat (Frankland, 1976). It seems likely that more mycelium will occur in the deeper organic layers of a mor site than in a mull, but Hering (1982) recorded similar quantities (fresh weights) of the basidiocarps on these two humus types when he surveyed comparable sites. It is most common on broadleaf- and needle-tree litter, but it colonises many other plant materials in its path including small woody components such as twigs and beech husks. Particularly in dry forests, the basidiocarps often arise from moist mats of moss, but the origin of the stipe can often be traced back to fragments of tree litter.

The lack of resource-specificity is confirmed by the large number of litter types on which *M. galopus* has been grown, including litter of several tree species, herbs, grasses, ferns and mosses (Hintikka, 1961; Hering, 1967; Frankland, 1969, 1975). However, it did not utilise *Mercurialis* (pH 6.4), and growth on *Calamagrostis* (pH 7.2) and *Cirriphyllum* (pH 8.2) was delayed. Hintikka attributed this to an initially unfavourable pH followed by amelioration of the condition through fungal activity. In the field, he recorded *M. galopus* growing on litter at pH 4–5.2, and in pure culture the optimum was pH 4–5, some growth occurring over a much wider range. A decrease in pH during decomposition by this fungus has been recorded in most of the litters tested; in bracken it fell by as much as one unit (pH 5.3 to 4.3) in 12 months.

The bulkier woody components of the forest floor are rarely colonised, probably because the mycelium is not adapted to conditions in the interior where aeration is restricted and various inhibitory substances tend to accumulate. In contrast to several typical lignicolous basidiomycetes, growth was almost totally inhibited by a concentration of 30% CO₂ in the atmosphere, and it was intolerant of relatively low concentrations of acetates in laboratory experiments (Hintikka, 1969, 1982; Hintikka & Korhonen, 1970).

A secondary colonist

M. galopus appears to have the potential to attack all the major constituents of plant litter. Lignin, α -cellulose, hemicelluloses, protein and soluble carbohydrates in plant litter, and purified xylan and pectin, have all been degraded by it in the laboratory (Hintikka, 1961, 1970;

Hering, 1967; Frankland, 1969). Further evidence of its capabilities as a decomposer comes from the detection of enzyme production, including that of polyphenol oxidases, cellulases and catalase (Lindeberg, 1948; Lamaison, 1976), but the extent to which these enzymes are exocellular needs further investigation.

The lack not only of resource specificity but also of substrate specificity (as shown in the absence of competitors) may suggest an even wider rôle for this saprotroph than is realised in nature. It holds a major position with other basidiomycetes in litter, but it is above all a *secondary* colonist, predominating at later states of decomposition and degrading cellulose and lignin to form a typical white rot. This pattern of behaviour follows a 'combative ecology strategy' (see Rayner & Webber: Chapter 18). The exact time at which a fungus arrives on a resource is usually difficult to determine. I have recorded the mycelium in the phylloplane of *Fraxinus excelsior* but only rarely; it probably originated from aerial spores before other micro-organisms closed in, and it may well have failed to survive. First recordings were usually obtained at a much later stage in the decomposition. On bracken petioles, *M. galopus* appeared in the first year of decomposition, and it was not fully established until the second year, after other species had destroyed much of the epidermis, phloem and non-lignified cortex and had opened up the interior (Frankland, 1966). These other organisms may have actually paved the way for the basidiomycete. Such a mechanism of species replacement corresponds with the *obligatory succession* and *facilitation model* described for higher plants (Frankland, 1981), and with '*stress alleviation*' during the development of a fungal community as discussed by Cooke & Rayner (1984) – see Rayner & Webber: Chapter 18. Similarly, it has been argued that *M. galopus* primes the resource for the next species when it produces soluble carbohydrates by hydrolysis of cellulose. However, such preconditioning, if it occurs, is very difficult to prove (Rayner & Webber: Chapter 18).

A rapid decline in the lignin and cellulose contents followed the colonisation of bracken petioles, and 'bore-holes' resembling those formed by wood decomposers were formed in the fibre walls around the hyphae. Confirmation that *M. galopus* was the agent responsible for this aggressive attack was obtained from axenic cultures on gamma-irradiated bracken; cavities of the same type were formed in the fibres, and breakdown of 25% lignin, 32% α -cellulose and 54% hemicellulose had occurred in one year.

Table 1. *Decomposition by Mycena galopus of α -cellulose in leaf litter of different tannin contents*

Litter	Soluble tannins (mean % \pm S.E., $n = 5$)	Loss ^a of α -cellulose (%)
Recently fallen		
<i>Quercus petraea</i>	9.5 \pm 0.1	5.0 NS
<i>Corylus avellana</i>	5.8 \pm 0.1	23.6*
<i>Fraxinus excelsior</i>	3.8 \pm 0.2	27.3*
<i>Betula pendula</i>	2.8 \pm 0.1	21.7***
After 6 months in the litter layer		
<i>Q. petraea</i>	2.9 \pm 0.0	43.4*
<i>C. avellana</i>	1.4 \pm 0.1	40.0***

^a Loss from gamma-irradiated samples inoculated with *M. galopus* compared with control samples after 6 months at 11 °C; absolute values.

NS: Not significantly different from controls.

Significance of difference from controls: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

The secondary colonisation by *M. galopus* of four broadleaf litter types (*Betula*, *Corylus*, *Fraxinus* and *Quercus*) has also been followed by taking samples directly from the litter layer in a UK woodland with mull humus (Frankland, Bailey & Costeloe, 1979). The basidiomycete became prominent earlier than on bracken, the exact timing depending on the species of litter. On *Fraxinus*, a quickly-decomposing litter already well attacked before leaf-fall, the period extended from 0 to 6 months; on *Betula* and *Corylus* from 6 to 12 months, and on *Quercus*, the most slowly decomposing litter, from 6 to 18 months or more after leaf fall. Removal of tannins may be a prerequisite. Growth of the mycelium has been shown to be inhibited by tannins in *Quercus* litter, which has a relatively high content of these substances (Harrison, 1971), and the ability of the fungus to degrade α -cellulose in sterilised litter was greater in 'weathered' than recently fallen leaves with higher tannin contents (Table 1).

In the compacted litter of a coniferous forest decomposing under mor conditions and bound together by fungal mycelium, the relationship between individual resource units and a particular species is less obvious, but the location of the mycelium was deduced by tracing the origin of basidiocarps. In this way, *M. galopus* was found to fruit

consistently from the F₁ horizon of a *Picea sitchensis* plantation (Newell, 1948a), and it could be assumed that active mycelium predominated on needles which were still whole but lacking mesophyll and extensively colonised by other fungi. Again, a preparatory phase of decomposition appears to have been necessary.

Competitive interactions

Success for *M. galopus* in the capture of secondary resources must depend on a complex network of interactions. It grows in close proximity not only to many microfungi but also to other saprotrophic agarics, including closely related species with overlapping niches. Tightly mixed clumps of the basidiocarps with those of *Collybia*, *Cystoderma*, *Marasmius* and other *Mycena* species have been described (Newell, 1980; Swift, 1982), and the mycelia of such neighbours must be in positions where they will compete for limited nutrients and space. How then is a competitive balance maintained?

As a secondary colonist, *M. galopus* is likely to be more adapted to combative competition than a pioneer (see Frankland, 1981; Cooke & Rayner, 1984; Rayner & Webber: Chapter 18). The basidiospores germinate readily on laboratory media, but subsequent growth is relatively slow, especially on litter, unlike that typical of some earlier, non-combative, colonisers with diffuse scavenging mycelia. Invasion by migrating mycelia rather than spores, and a relatively high inoculum potential, provided in *M. galopus* by densely branched and often aggregated hyphae, should favour establishment on a resource which is no longer virgin territory. Once established, it needs to withstand its neighbours for long periods while exploiting refractory substances. Mechanisms underlying this combative type of competition can be grouped in terms of antibiosis and contact reactions between hyphae and between mycelia (Rayner & Webber: Chapter 18). Features indicative of such mechanisms were seen in cultures of *M. galopus*, but few facts are known regarding their expression in the field. Antibiotics have not been detected, but there is an unconfirmed record of antibiotic activity against *Escherichia coli* (Mathieson, 1946), and an unusual report of viral inhibition by a liquid medium in which the fungus had been grown (Villard, Oddoux & Porte, 1979; Villard, Porte & Oddoux, 1982). Contact antagonism is common, and interaction zones occurred regularly on both nutrient media and litter in pairings against several basidiomycetes frequently associated with *M. galopus* (J. C. Frankland, unpublished). In these zones, the hyphae grew abnormally, often

producing pigments and mycelial barrages were formed. *Mycena epiphytygia* eventually grew over *M. galopus* after an initial check, but deadlock between a pair was more usual. This strongly interactive character could be an important means of holding a territory and preventing replacement by a competitor (see Rayner & Todd, 1979; Frankland, 1981), although 'zone lines' in field litter occupied by this species were rarely as distinct as those produced by wood fungi.

Acidification of the resource by the fungus (p. 245) could also be an advantage by restricting bacteria, but some laboratory evidence suggests that streptomycetes in *Picea* litter can antagonise *M. galopus* (Dickinson, Dawson & Goodfellow, 1981). On *Quercus* litter, however, living and dead hyphae were remarkably resistant to attack by the natural microflora, 25% of hyphae tagged with brightener surviving for more than a year in the field (Frankland, 1975; Frankland *et al.*, 1979).

The final outcome of competition will depend on the balance between competitive ability and the inoculum potential – the energy of growth available for colonisation. This is illustrated by the hypothesis proposed to explain the relative distributions of *M. galopus* and *Marasmius androsaceus* (possessing rhizomorphs) in a plantation of *Picea sitchensis* in Grizedale Forest, in the English Lake District (Newell, 1980, 1984a,b). The *Mycena* might appear to be a weak contender as regards inoculum potential compared with species which form rhizomorphs or cords, unless the involvement of factors such as grazing pressure which control hyphal density and age is considered, as by Newell.

In the laboratory, *M. androsaceus* appeared to have superior competitive abilities. Its mycelial production and growth rate on a nutrient medium was about 30–50% more than that of the *Mycena*, and its colonisation and decomposition of sterile spruce litter were also significantly greater. When litter inoculated with one or other of the two species was mixed in different ratios and 'seeded' with sterilised spruce needles (equivalent to a primary resource), colonisation of the latter by *Marasmius* was even greater than expected (Fig. 1).

Nevertheless, in the plantation where the two species were close enough to interact, the basidiocarps were equally abundant. In mixed-species clumps, however, the mean depth at which *M. galopus* fruited increased from 6 mm in single-species clumps to 10 mm ($P \leq 0.05$), whereas that of *M. androsaceus* remained at 1 mm, suggesting that the mycelia were zoned vertically (Fig. 2). This discovery led to an examination of the effect of grazing by a small yellow collembolan, *Onychiurus latus*. It was the most abundant mycophagous arthropod on

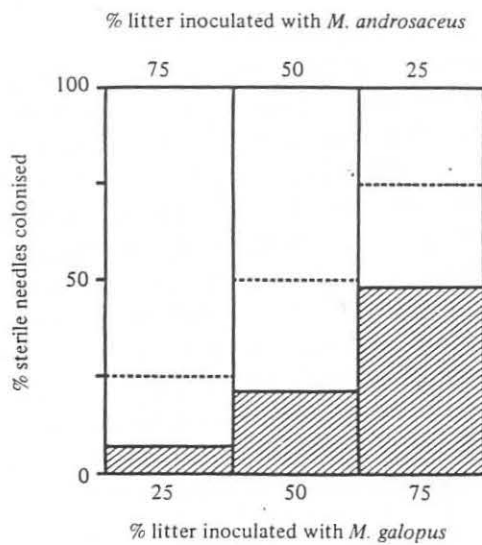


Fig. 1. Colonisation of sterile spruce litter by *Mycena galopus* and *Marasmius androsaceus* after 24 days at 11°C in mixed cultures, initially 'seeded' with the two fungi on litter in three different ratios (from Newell, 1980). Hatched area, *M. galopus*; open area, *M. androsaceus*; --- expected result if colonising abilities had been equal. (From Newell, 1980.)

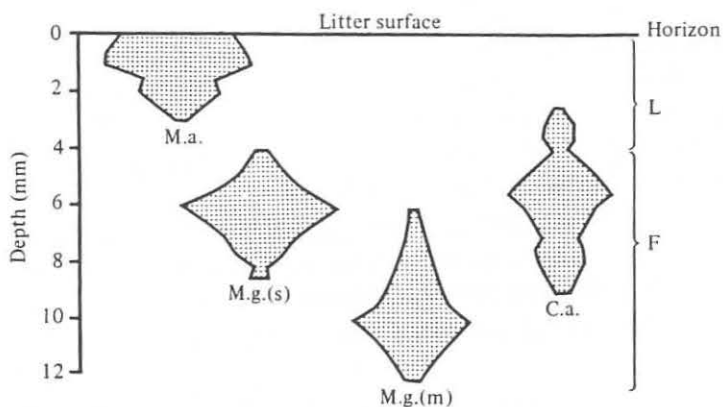


Fig. 2. The fruiting depths of *Marasmius androsaceus* (M.a.), *Mycena galopus* (M.g.) and *Cystoderma amianthinum* (C.a.) in a *Picea sitchensis* plantation. The width of each 'kite' at any depth is proportional to the percentage number of basidiocarps originating at that depth. s, single-species clumps of *M. galopus*; m, mixed-species clumps of *M. galopus* with *M. androsaceus*. (From Newell, 1980.)

the site and its gut consistently contained basidiomycete mycelium. Migration of the animal up and down the profile was related to its life cycle and the moisture content of the litter.

O. latus showed a marked preference for the mycelium of *M. androsaceus* both in the laboratory (Fig. 3) and the field, and a population of 10 specimens per gramme of air-dried litter in mixed cultures of the two fungi on litter could alter the outcome of competitive colonisation in favour of *M. galopus* (Fig. 4). The mycelial characters affecting the palatability and selective grazing of these species are not known.

In field tests, an increase in the density of the collembolan resulted in an increase of *Mycena* basidiocarps and a decrease of those of *Marasmius*, whereas a decrease in density had the reverse effect.

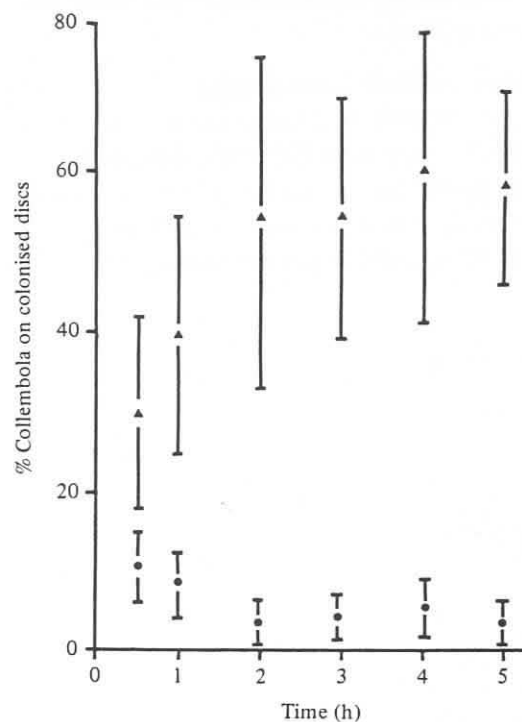


Fig. 3. The percentage number (\pm s.e.) of *Onychiurus latus* which had migrated onto agar discs covered with mycelium of *Mycena galopus* (●) or *Marasmius androsaceus* (▲) after increasing time intervals. Total number of animals released = 250; each of 10 replicate dishes contained 25 animals and both food sources. After 5 h, 5% of the aerial mycelium of *M. galopus* had been grazed and 72% of that of *M. androsaceus*. (From Newell, 1984a.)

Newell's experiments and observations led to the following hypothesis to explain the zonation of the mycelia: selective grazing of *M. androsaceus* mycelium altered the outcome of competition in the F₁ horizon sufficiently to allow *M. galopus* to predominate in that horizon, but in the L horizon the density of the Collembola was not great enough for a sufficiently long period of time to alter the competitive balance, with the result that the *Marasmius* mycelium was more abundant. The hypothesis needs to be tested further bearing in mind the differences between a sterile and an inhabited secondary resource, but it is one example of how a competitive balance could be maintained, and it indicates the major importance of animal/fungal interactions in the ecology of a mycelium. More recent research (Dix, 1984) showing that *M. galopus* is less tolerant than *M. androsaceus* of low water potentials introduces another relevant factor.

Spatial distribution and individual mycelia

The interaction study built up a picture of the vertical distribution of the mycelium of *M. galopus* in Grizedale Forest, but less was known about its logistics across the forest floor. Clumps of basidiocarps 1–3 m in diameter were described by Newell, but rings were not observed. In deciduous woodlands, Parker-Rhodes (1954) concluded

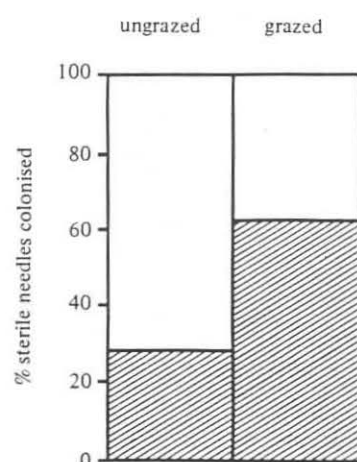


Fig. 4. The colonising abilities of *Mycena galopus* (hatched areas) and *Marasmius androsaceus* (open areas) with and without grazing by *Onychiurus latus* (20 per replicate), after 24 days at 11°C in mixed cultures. These initially contained equal quantities of litter inoculated with each of the two fungi and 10 sterile spruce needles per replicate. (From Newell, 1984b.)

Table 2. Percentage number of basidiocarps occurring in each one-third band of a permanent plot in three successive years

Year Band	1	2	3
1	30.1	38.4	36.7
2	45.9	47.3	49.5
3	24.2	14.4	13.8

that populations were polymorphic and Swift (1982) found possible evidence of slight annual 'movement' in the spatial pattern of fruiting. More intensive mapping of the basidiocarps combined with preliminary genetical analysis of a population in the spruce plantation has, however, given some indication of the size and distribution of individual mycelia (J. C. Frankland, unpublished).

The positions of the basidiocarps in a permanent plot (10 × 4.5 m) were mapped using a grid system of 5 mm coordinates; the caps were painted to prevent stimulation of fruiting by their removal or repeated recordings. Data accumulated over five fruiting seasons were then analysed by computer programs. Complete absence of a ground flora greatly facilitated the recording, but the irregular and close spacing of the spruce trees was likely to have complicated the distribution patterns more than did the regular tree plantings examined by mycorrhizalists in similar mapping projects (Mason, Last, Pelham & Ingleby, 1982).

In 'good' seasons at least 1000–2000 basidiocarps were produced on the plot, indicating the presence of abundant mycelium in the litter, especially if it is assumed that the ratio of the production of basidiocarps:production of vegetative mycelium was 1:10, as calculated for *Quercus* litter (Frankland, 1975).

The basidiocarps were not distributed randomly over the plot. This was tested by dividing the plot into thirds and calculating the number of basidiocarps in each one-third band as a percentage of the total in the plot in three successive years. The percentages in a particular band were approximately constant but significantly different between bands, indicating non-randomness (Table 2).

M. galopus basidiocarps are ephemeral, usually lasting only 2–3 days. Distinctive spatial patterns were not therefore picked out by on-the-spot observations, but accumulated annual data when plotted and superimposed revealed some arcs or partial annuli of basidiocarps, each apparently related to the position of a tree. Two of these arcs are illustrated in Fig. 5. They might have been expected if the species had

been mycorrhizal instead of saprotrophic, but various factors such as inhibitors in stem flow, nutrients in drip from the canopy, and litter depth could have been responsible and need investigation.

Slight annual changes in the overall position of fruiting zones of the mycelium even if not of whole colonies were sometimes suggested if 0.5 m² subplots were compared in different years as in Fig. 6. However, comparison of coincident basidiocarp positions over the whole plot in successive and non-successive years indicated stability (Fig. 7). The number of basidiocarps which coincided within ranges of 0–20 mm with positions mapped in a previous year is represented by histograms. In the example of successive years, only seven basidiocarps (total number: 993) coincided exactly with a basidiocarp of the previous year. Coincidences increased as the range increased, but, if due weightings were

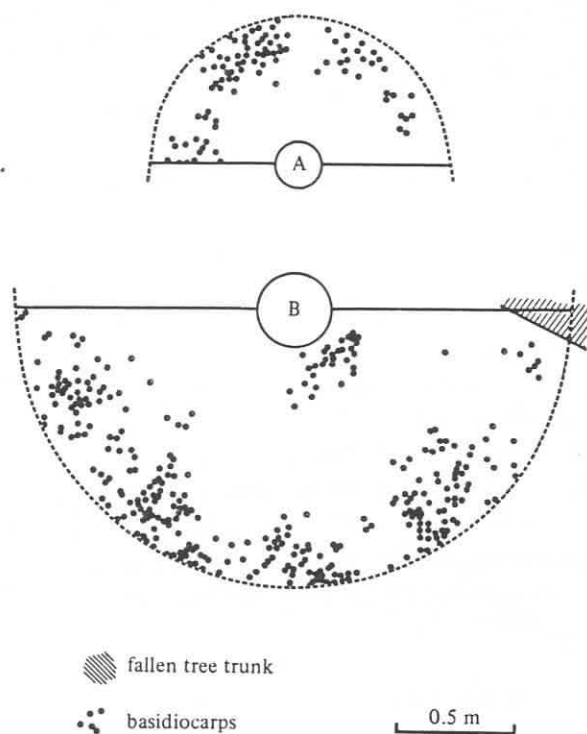


Fig. 5. Annuli of basidiocarps of *Mycena galopus* around two trees (A, B) of *Picea sitchensis*. Four-year records superimposed. Dashed line, arbitrary circular boundary with the tree as centre, cutting off basidiocarps close to neighbouring trees.

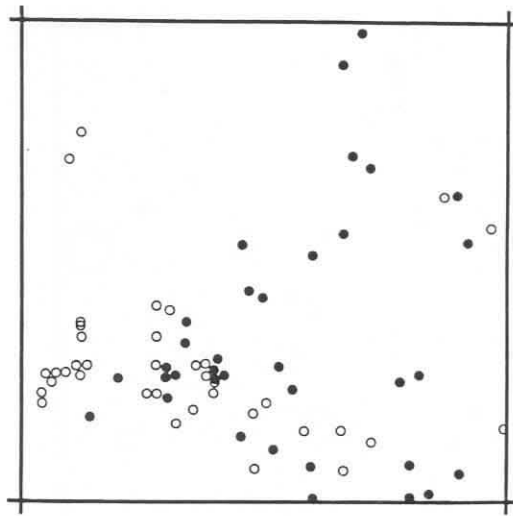


Fig. 6. Mapped positions of *Mycena galopus* basidiocarps on a 0.5 m² spruce plot, suggesting a slight shift in time; 1978 (filled circles) and 1981 (hollow circles) records. The distribution pattern of records from the intervening period was 'intermediate' between those of 1978 and 1981.

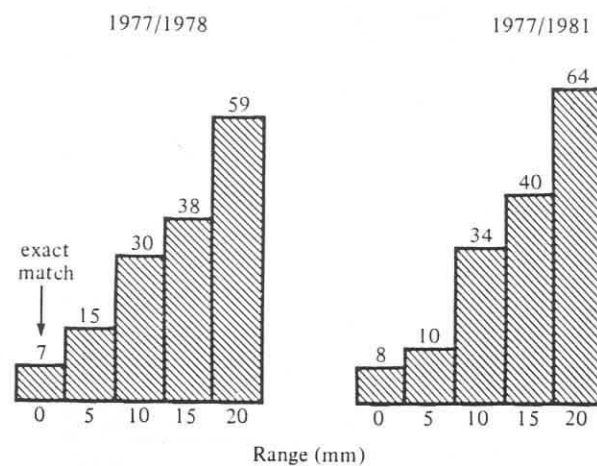


Fig. 7. The numbers of basidiocarps of *Mycena galopus* in a spruce plot which coincided in successive and non-successive years within ranges of 0–20 mm of 1977 positions.

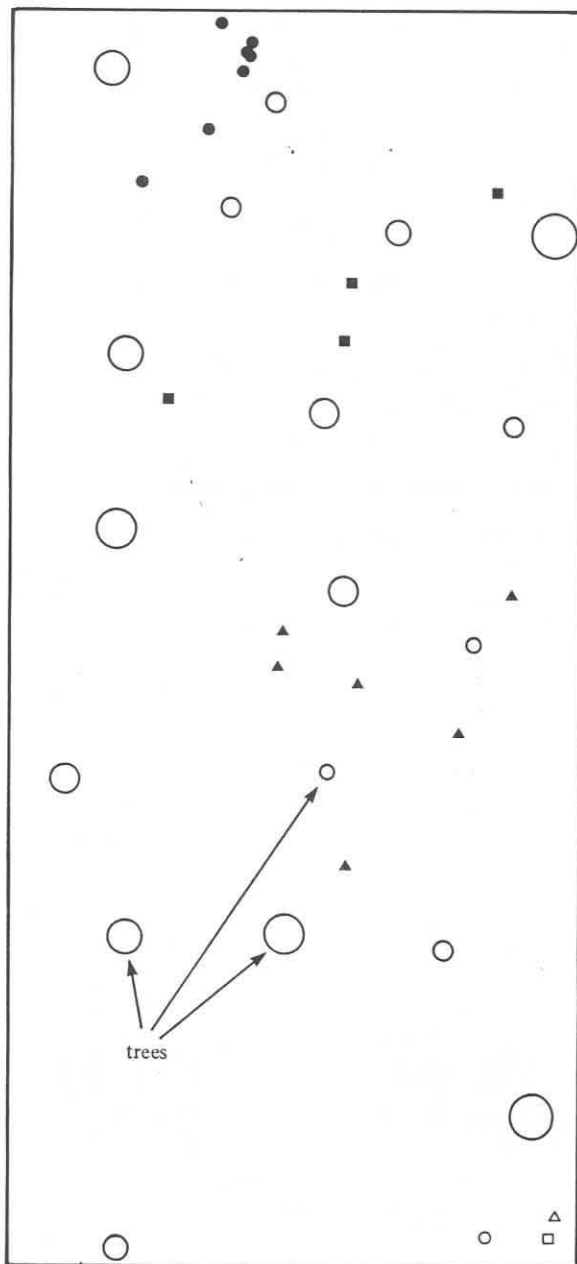


Fig. 8. Individual mycelia of *Mycena galopus* in a 10×4.5 m plot of *Picea sitchensis*. Dikaryotic isolates which fused imperceptibly are represented by the same symbol (filled circles, squares and triangles).

made for seasonal differences, they did not decrease in comparisons of non-successive years. All the evidence pointed to perennial or at least renewable mycelium occupying the same locations from year to year.

It is now clear that distinct individual mycelia exist in populations of heterothallic wood-decomposing basidiomycetes (Rayner & Todd, 1979; Thompson & Rayner, 1982). On this basis, the population structure of this litter decomposer on the spruce plot was investigated by examining the interactions between mycelial isolates using similar procedures. Only preliminary findings are reported here, and mating-type factors need further investigation. Forty dikaryotic mycelia were obtained from stipe tissue by dissecting hyphae from the interior of the stipe, or by plating stipes on 2% malt agar, after surface sterilisation in 10% (v/v) aqueous sodium hypochlorite.

As in similar studies, the isolates could be grouped according to whether or not they intermingled or exhibited various degrees of antagonism when paired. Three relatively large individual mycelia or mycelial types appeared to be recognisable by such groupings (Fig. 8), surrounded on the plot by numerous smaller individuals, which it could be surmised had arisen from spores or formed the edge of individuals outside the plot. Sampling was too limited to cover completely the areas occupied by arcs of basidiocarps or to relate them with any certainty to particular mycelial types. The greatest distance on the plot between two basidiocarps producing intermingling isolates was approximately 2.5 m.

The number of individual mycelia on the small spruce plot appears to be proportionally far greater than that of *Tricholomopsis platyphylla* found on an area of 2.1 ha by Thompson & Rayner (1982) (see also Chapter 9; Fig. 4). This possibly reflects a different colonisation strategy on a coniferous litter resource which would be constantly changing as new supplies fall from the canopy. The large perennial individuals on the plot are consistent with the theory of a *K*-selection strategy for basidiomycetes (Swift, 1982; Rayner & Webber: Chapter 18).

It is easy to see that *M. galopus* is common in many temperate woodlands. The overall attainments of the whole fungus as a competitive colonist are less obvious, but often striking. In one UK woodland,

Caption for Fig. 8 (*cont.*)

One of several small incompatible groupings is shown in the bottom right-hand corner of the plot (small hollow circle, square and triangle).

more than 80% of the leaves of the dominant *Quercus*, two years after leaf-fall, were found to be colonised by the mycelium when it was induced to fruit (Frankland, Bailey & Costeloe, 1979), and it has been estimated that this fungus decomposes a considerable proportion of the annual litter fall in British woodlands (Hering, 1972). Smith (1947) in his monograph described it as looking 'like a very ordinary slender gray or blackish *Mycena*'. Maybe, but it is a remarkably successful species.

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